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SECTION OF WILDLIFE ECOLOGY ON PUBLIC LANDS
DENVER WILDLIFE RESEARCH CENTER
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ANNUAL PROGRESS REPORT

Energy expenditure of moose on the Kenai National Wildlife Refuge,

by

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in cooperation with

ALASKA DEPARTMENT OF FISH AND GAME

FEDERAL AID IN WILDLIFE RESTORATION PROJECT W-17-11

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WORK UNIT TITLE: Energy Expenditure of Moose on the Kenai National Wildlife Refuge

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SUMMARY

The objective of this work unit is to measure the energy requirements of moose during different seasons and for different sex and age classes. Techniques employed will permit partitioning of the energy contained in plants into various components down to net energy available for production. This information, along with data collected on forage supply and quality in a companion study, will be used in a mathematical model which can predict the capacity of the Kenai National Moose Range to support moose. This report summarizes the work completed prior to May 1981. Results include food intake rates, digestion trials, rumen turnover time, seasonal energy expenditure, methane production, simulation modeling, and energy partitioning.

BACKGROUND

A study to develop a carrying capacity model for moose was initiated in 1977 as a cooperative research project by the DWRC and the Alaska Department of Fish and Game (ADF&G). Carrying capacity is the capability of a range or area to support animals. New concepts to estimate carrying capacity are based on an understanding of nutrition and bioenergetics. They were developed by Moen (1973) and refined by Robbins (1973) and Wallmo et al. (1977). The idea is to determine the amount of nutrients the animal requires for its metabolic functions and measure the quantity and quality of these nutrients available in the habitat. Mathematical equations can then be developed to estimate the carrying capacity.

This work unit covers all studies related to the animal requirement portions of the model. The concepts of how individual studies will be integrated into a mathematical model are explained in a compendium of

Research Projects Related to carrying capacity (Regelin 1978). The research is conducted at the Moose Research Center (MRC).

OBJECTIVES

Specific objectives of this work unit are to:

1. Measure the fasting heat production (FHP) of adult moose during different seasons and compare FHP of male and female moose.
2. Determine the heat increment (HI) of moose during each season and when fed different diets.
3. Measure the energy lost as methane for different diets.
4. Partition the flow of energy through an adult moose during different seasons and for different diets.

Objectives of the companion studies being conducted by the ADF&G are to:

5. Develop a feed ration capable of maintaining moose.
6. Determine minimum and optimum crude protein requirements for various sex and age classes of moose on a seasonal basis.
7. Measure rumen turnover time, rate of passage, and rumen volume of moose.
8. Determine the daily activity budget of moose by season.
9. Determine the effects of various levels of nutrients on blood parameters.

PROCEDURES

The methods used to meet objectives 1-4 were described in the Work Unit Outline entitled Energy Expenditure of Moose on the Kenai National Moose Range. A detailed description of the metabolic chamber and the procedures used to measure fasting heat production was prepared by Regelin et al. 1982 (see Appendix A).

Procedures for objectives 5-9 were described by Schwartz and Franzmann 1981a, b.

Carrying Capacity Model and Simulation Experiments

One goal of the moose nutritional physiology studies is to provide data for use in a carrying capacity model. The model we are using was developed by David Swift, Natural Resources Ecology Laboratory, Colorado State University. The structure of the model is shown in Fig. 1. It is a generalized model for nitrogen (N) and energy balance for nonreproductive

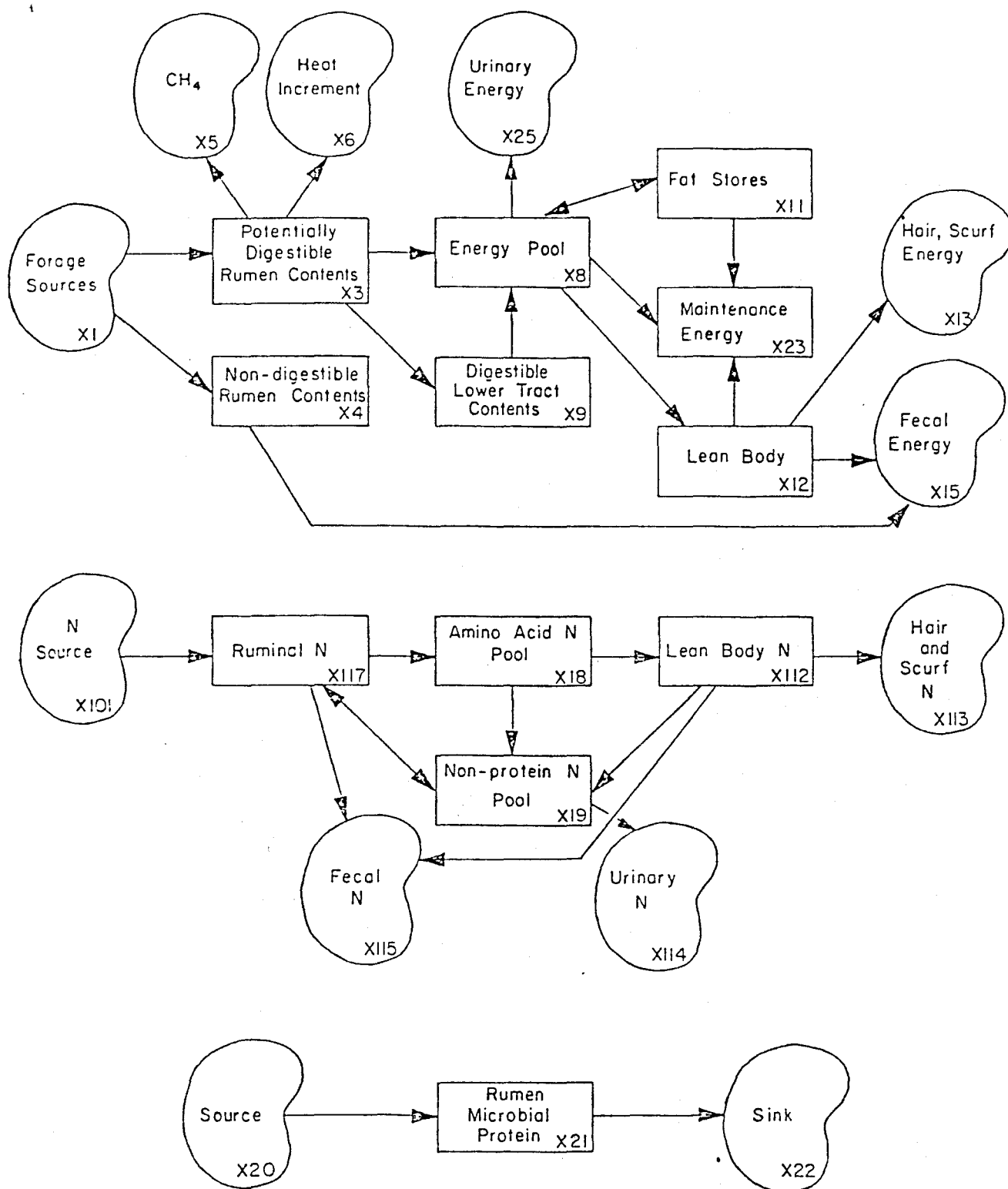


Figure 1. The structure of the ruminant submodel.

ruminants. Energy and nitrogen costs to the animal are simulated along with the voluntary intake and metabolism of these nutrients. This permits time traces of lean body mass and fat reserves to be developed so changes in body weight and composition can be followed. The model is a difference equation model with a one-day time step.

The model is driven by input time traces of the dietary N concentration, digestibility values, and daily maximum-minimum temperature. The model requires 47 input parameters, 15 of these were altered to make the model specific for moose (Table 1). The remaining input parameters are not species dependent, or information specific to moose was lacking and values for domestic livestock were utilized.

Simulation experiments were run for wintering moose (1 November - 30 April) on the computer at Colorado State University in January 1981. Nine baseline runs (simulation) were performed altering inputs until a standard baseline was obtained which approximated what we felt was a "real" simulation of moose weight loss during winter. Values used for the baseline simulation are shown in Table 1. These values were based upon data collected at the MRC or literature sources. Fat reserves were assumed to be 25% of total body weight in the fall.

Experimental runs were conducted by increasing or decreasing the following driving variables or input parameters: Daily activity, initial fat reserves, dietary N concentration, dry matter digestibility of the diet and metabolic fecal N. Each of these parameters was altered separately to determine the importance of that variable upon the winter metabolism of moose.

FINDINGS

Experimental Moose Feed

A ration suitable for maintenance of moose has been developed at the MRC (Schwartz et al. 1980). Formulation of such a ration was a necessary prelude to meeting the objectives of this study. Few moose have been held in captivity because no feed had been successful in maintaining healthy moose. This ration, referred to as the MRC Special, has been used exclusively to maintain eight moose for the past 3 years. Health of these moose has been excellent based upon weight gain and reproductive success.

The MRC Special was formulated to provide nutrients in approximately the same amount as the native forages eaten by moose. The "key" ingredient is aspen sawdust (Table 2). The wood fiber provides the proper ratio of fiber components. The ration has a digestibility of 64% with a crude protein content of 11.75% (Table 3).

The MRC Special is being used to maintain moose at the University of Alberta and several zoos in the U.S. and Europe.

Table 1. Input data used in the baseline run for adult female moose as a standard for experimental runs.

Parameter	Input	Source of data
Dietary crude protein (%)		
Nov.-Dec.	7.4	Oldemeyer (1974)
Jan.-Feb.	6.1	Oldemeyer et al. (1979)
March	5.0	Regelin, W. unpubl. data
April	7.5	
Dietary digestibility (%)		
Nov.-Dec.	40	Oldemeyer (1974)
Jan.-Feb.	36	Oldemeyer et al. (1979)
March	34	Regelin, W. unpubl. data
April	39	Schwartz et al. 1981
Endogenous urinary nitrogen	.115 (wt).75	Robbins et al. (1974)
Metabolic fecal nitrogen	5 g Nitrogen/kg intake	Agricultural Research Council (1965)
Methane production (average)	5.0% of gross energy	Regelin, W., unpubl. data
Fasting metabolic rate (BMR)	90 (wt).75	Regelin, W., unpubl. data
Initial lean body (kg)	307.6 kg	Franzmann et al. (1978)
Initial fat weight (kg)	100 kg	Estimated: this is 24.5% of total body weight
Age at start of run (days)	2130 (5 yr, 4 mo)	Assume birth date of 1 June; trial runs began 1 November
Maximum life span (yr)	11	Estimated
Wind chill (c)	5	Renecker et al. (1978)
Lower critical temp (c)	-20	Renecker et al. (1978)
Winter cost of activity	1.5 (BMR)	Moen (1976) estimated
Rate of passage (%/Day) of digestible portion	70	Schwartz et al. 1981
Fraction of undigested (%/Day) material passing rumen	60	Schwartz et al. 1981

Table 2. Composition of the "MRC Special" diet formulated for captive moose.¹

Ingredient	Percent
Corn, ground yellow	30.0
Sawdust ²	22.5
Oats, rolled	25
Soybean meal, powdered	7.5
Cane molasses, dry	7.5
Barley, ground	7.5
Vitamin premix ³	T
Trace mineral salt ⁴	T
Dicalcium phosphate ⁵	1.3
Pelaid ⁶	T
Mycoban ⁷	T

¹ The diet was formed in 4.8-mm pellets.

² Aspen byproduct (Fiberlite, American Excelsior Co., Arlington, TX).

³ Each kg contained 5004.4 USP units vitamin A, 13228 IC units vitamin D₃, and 44 I units vitamin E.

⁴ Guaranteed analysis: NaCl 95-98%, Zn 0.35%, Mn 0.28%, Fe 0.175%, Cu 0.035%, I 0.007%, Co 0.007%.

⁵ Guaranteed analysis: P 18.0%, Ca 31.0-34.0%.

⁶ Pelaid, Rhodeia Inc., Ashland, Ohio, is a wood byproduct used to enhance pelleting.

⁷ Mycoban, Van Waters and Rogers, Anchorage, Alaska, inhibits mold growth. T = 0.5 lb/ton (0.025%).

⁸ Data from Schwartz et al. 1981.

Table 3. Chemical composition and apparent digestibility of the "MRC Special" diet formulated for captive moose.

Analysis	Amount and units
Dry matter	90.0%
Crude protein	11.75%
Cell wall constituents	47.2%
Acid-detergent fiber	26.5%
Gross energy	4.45 Kcal/gram
Calcium	9750 ppm
Potassium	7140 ppm
Sodium	2910 ppm
Phosphorus	2106 ppm
Magnesium	205 ppm
Iron	62 ppm
Zinc	23 ppm
Copper	6 ppm
Selenium	0.22 ppm
Cobalt	0.1 ppm
Chromium	0.1 ppm
Dry matter digestion (in vivo)	64.3%

Data from Schwartz et al. 1981.

Feed Consumption

Intake rates of tame moose fed the MRC Special were measured periodically for the past 3 years (Table 4). Feed consumption varied seasonally with highest intake during summer and low intake during the breeding season and late winter (Fig. 2). Intake rates were similar for males and females except during the "rut" when males stopped eating for 12 days. Consumption during summer averages about 23 g per kg of body weight. This value is similar to that estimated for mule deer (Aldredge et al. 1974). Intake rates during winter decreased from early winter to a low in early spring just prior to initiation of plant growth (Table 4, Fig. 2).

Digestion Trials

Four complete digestion and balance trials were conducted during the past year. During the first two trials, the moose were fed the MRC Special with a mill byproduct (Fiberlite, American Excelsior Co., Arlington, Texas) used as the source of aspen sawdust. The third trial was conducted feeding the tame moose a mixture of 40% aspen (Populus tremnoides) clipped during winter and 60% MRC Special. During trial number four the moose were fed a browse diet containing equal amounts of birch (Betula papyrifera), aspen, and willow (Salix spp.) by wet weight.

Three female moose were fed the diet in trial one; two male moose were used in trial two. Results of these trials (Table 5) indicated higher gross energy intake levels but lower net energy retention (gross energy-fecal energy) for females when compared to males. We suspect that these differences were a result of factors other than differences of efficiency levels between sexes. The dry matter digestion (DMD) trial using the two males was conducted post rut, during the period when the two males were increasing their intake levels back to normal. We believe the higher digestion of dry matter was a result of dry matter being retained in the gut tract while the animals refilled the digestive tract. Both males stopped eating for 12 days, but continued to produce fecal material. As a result, we believe they voided most of the dry matter from the rumen and lower gastrointestinal tract during this fasting period. Since we measured intake and fecal output during the initial stages of resumed eating, much of the undigested dry matter was probably retained in the gut tract as bulk and not passed through as feces. The digestive coefficient of $56.4 \pm 12\%$ for the females probably more closely represents the true DMD of the Fiberlite byproduct ration.

The digestibility of the mixture of pelleted ration and aspen fed in Trial 3 had a total DMD of $57.3 \pm 4.4\%$. The variation in total digestibility was small. The ratio of aspen:feed consumed varied from 50 to 28% (Table 6). Although we attempted to balance the intake ratio at 40:60 aspen:feed, because the animals consumed various amounts of each, the ratio between animals was wide. Likewise this difference in consumption of aspen and feed was reflected in the total daily gross energy intake/day between animals. Chester preferred the aspen and readily consumed all that was offered. Chief and Lucy preferred the pelleted ration and ate less aspen;

Table 4. Seasonal daily intake of dry matter for moose on the MRC Special ration, moose born June 1978.

Animal	June 1-10, 1979				October 9-25, 1979			
	A	B	C	D	A	B	C	D
	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}
Angel	249	6093	24.5	97.2	326	4197	12.9	54.7
Lucy	243	5305	21.8	86.2	-	-	-	-
Chief	271	6305	23.3	94.4	328	5264	16.0	68.3
Rodney	273	6508	23.8	96.9	310	5364	17.3	72.6
Chester	247	6373	25.8	102.3	306	5312	17.4	72.6
Average	257	6116	23.7	95.4	317	5034	15.9	67.1
Average	264	6396	24.2	97.9	315	5313	16.9	71.7
Average	246	5700	23.2	91.7	326	4197	12.9	54.7
	November 10-19, 1979				March 5-11, 1980			
	A	B	C	D	A	B	C	D
	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}
Angel	323	7230	22.4	94.9	329	3955	12.0	51.2
Lucy	-	-	-	-	360	4107	11.4	49.7
Chief	333	6252	18.8	80.2	355	4383	12.3	53.6
Rodney	333	6579	19.8	84.4	356	4884	13.7	59.6
Chester	325	6552	20.2	85.6	336	4261	12.7	54.3
Average	328	6653	20.3	86.3	347	4318	12.4	53.7
Average	330	6461	19.6	83.4	349	4509	12.9	55.8
Average	323	7230	22.4	94.9	345	4031	11.7	50.4
	April 24 - May 5, 1980				July 2-11, 1980			
	A	B	C	D	A	B	C	D
	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}
Angel	-	-	-	-	-	-	-	-
Lucy	358	6238	17.4	75.8	323	8310	25.7	109.1
Chief	356	7515	21.1	91.7	383	8796	23.0	101.6
Rodney	350	5268	15.0	65.1	380	7930	20.9	92.1
Chester	334	6656	19.9	85.2	368	9470	25.7	112.7
Average	350	6419	18.3	79.5	363	8626	23.8	103.7
Average	347	6480	18.7	80.7	377	8732	23.2	102.0
Average	358	6238	17.4	75.8	323	8310	25.7	109.1

Table 4 - Continued.

Animal	September 6-14, 1980				October 6-10, 1980			
	A	B	C	D	A	B	C	D
	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}
Angel	364	9000	24.7	108.0	-	-	-	-
Lucy	359	9210	25.6	111.7	-	-	-	-
Chief	448	9100	20.3	93.4	-	-	-	-
Rodney	433	8000	18.5	84.2	384	4398	11.4	50.7
Chester	430	9960	23.2	105.5	381	1197	3.1	13.9
Average	407	9050	22.5	100.6	-	-	-	-
Average	437	9020	20.6	94.6	382	2798	7.2	32.3
Average	362	9105	25.2	109.8	-	-	-	-
	October 11-20, 1980				November 19-26, 1980			
	A	B	C	D	A	B	C	D
	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}
Angel	-	-	-	-	405	8062	19.9	89.3
Lucy	-	-	-	-	410	8228	20.1	90.3
Chief	-	-	-	-	426	8552	20.1	91.2
Rodney	384	6827	17.8	78.7	413	8749	21.2	95.5
Chester	382	7440	19.5	86.1	403	8131	20.2	90.4
Average	-	-	-	-	412	8344	20.0	91.3
Average	383	7134	18.6	82.4	414	8477	20.5	92.4
Average	-	-	-	-	408	8145	20.3	89.8
	January 23 - February 2, 1981				February 23 - March 4, 1981			
	A	B	C	D	A	B	C	D
	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}
Angel	406	8194	20.2	90.6	413	6632	16.1	72.4
Lucy	400	5823	14.6	65.1	404	6101	15.1	67.7
Chief	417	8951	21.5	97.0	418	5593	13.4	60.5
Rodney	395	8116	20.5	91.6	399	6588	16.5	73.8
Chester	391	7799	19.9	88.7	389	6666	17.1	76.1
Average	402	7777	19.3	86.6	405	6316	15.6	70.1
Average	401	8289	20.6	92.4	402	6283	15.7	71.1
Average	403	7008	17.4	77.8	408	6366	15.6	70.0
	April 6-19, 1981							
	A	B	C	D				
	Animal weight (kg)	Intake g	Intake g/kg wt	Intake g/kg ^{.75}				
Angel	413	7613	18.4	83.1				
Lucy	414	5709	13.8	62.2				
Chief	438	9670	22.1	101.0				
Rodney	397	8387	22.1	94.3				
Chester	379	8068	21.3	94.3				
Average	408	7889	19.5	87				
Average	405	8708	21.8	96.5				
Average	413	6661	16.1	72.6				

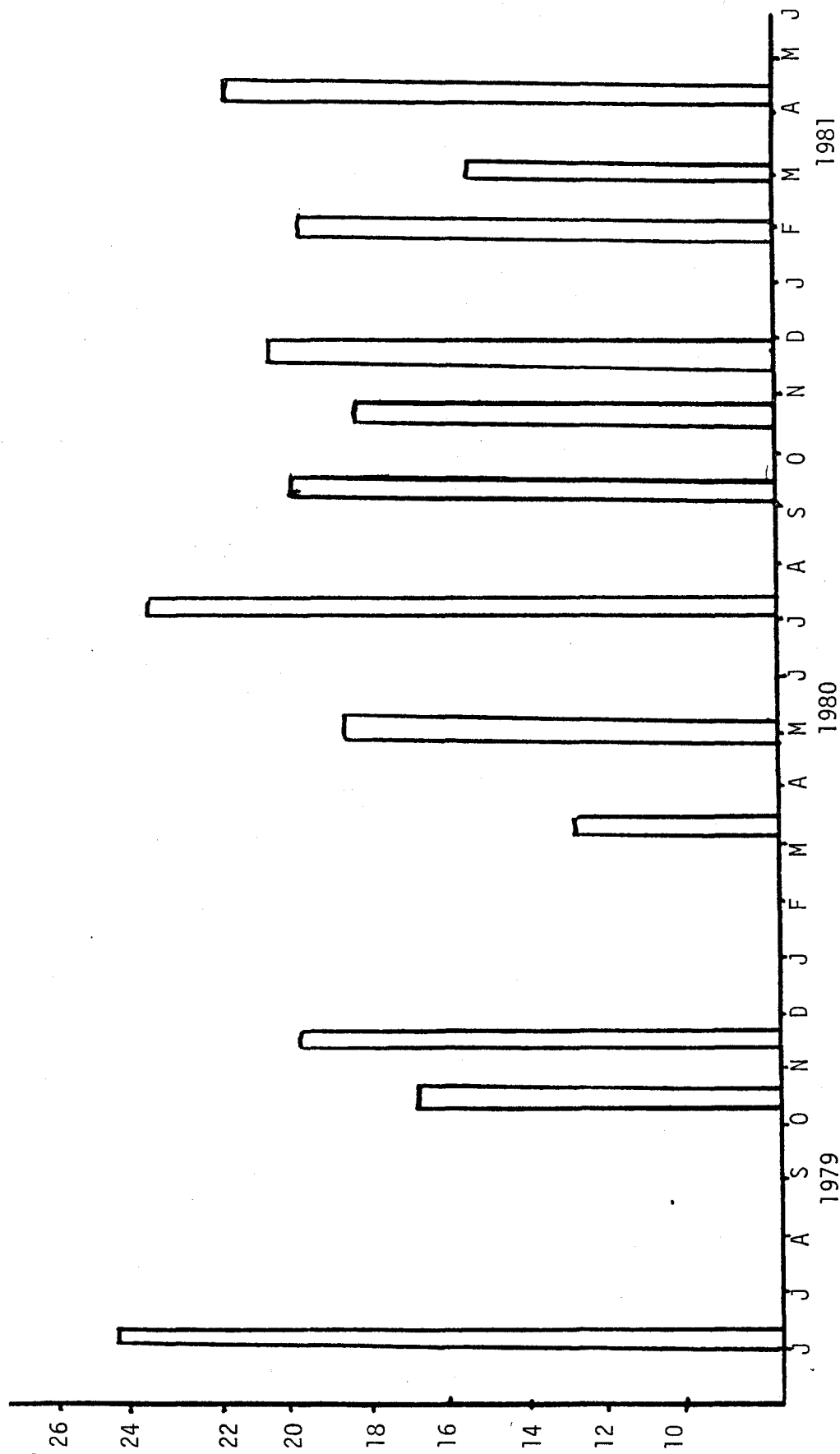


Fig. 2. Season intake rate of dry matter for moose fed the MRC Special ration.

Table 5. Gross energy intake and fecal energy loss for moose fed the MRC Special ration during October and November 1980.

Trial and animal	Body wt (kg)	Daily GE intake (kcal)	Fecal energy % GE intake	Digestibility %
Trial 1				
Angel	366	33622	43.3	56.7
Jezebel	320	22206	41.8	58.2
Lucy	371	26738	44.1	55.9
Trial 2				
Rodney	374	18361	32.3	67.7
Chester	381	17178	28.3	71.7

Table 6. Gross energy intake and fecal energy loss for moose fed a pelleted ration (MRC Special) and winter clipped aspen browse.

Animal	Body wt (kg)	Ratio of food consumed Aspen:pelleted ration	Daily GE intake/ Kcal	Fecal energy % GE intake	Calculated ¹ aspen digestibility %
Chief	350	30:70	16046	45.9	30.5
Chester	334	40:60	24430	41.6	46.8
Rodney	341	50:50	16727	41.2	51.4
Lucy	363	28:72	20258	39.4	45.6

¹ The DMD of aspen was calculated by assuming a 68% DMD for the pelleted ration and calculating mathematically the digestion coefficient for the aspen (i.e., the total DMD for the mixture was 59.5%, and Chester ate 60% feed:40% aspen, then $0.68 \cdot 0.60 + \chi \cdot 0.40 = 0.595$; $\chi = 46.8\%$). The 68.0% DMD for the pelleted ration was determined from a previous digestion trial (Schwartz and Franzmann 1981).

we therefore only offered them quantities of feed equivalent to the daily aspen intake, thus reducing total daily energy intake. We calculated the DMD of the aspen fed during this trial mathematically. We assumed the DMD for the pelleted ration was 68.0% as previously determined in a digestion and balance trial (Schwartz and Franzmann 1981).

The following calculations were made: $0.68 \cdot \% \text{ feed ration} + \% \text{ aspen}$

$$X = \text{Total DMD}; \text{ then } \% \text{ DMD of aspen} = \frac{\text{Total DMD} - 0.68 \cdot \% \text{ Feed}}{\% \text{ Aspen}}$$

With the exception of Chief, the calculated digestion coefficients for aspen were similar (Table 6). We have no explanation why Chief differed. With the exception of Lucy, another trend in the data appeared to indicate increased DMD of aspen with an increased percentage in the diet. The percentage of aspen consumed for Rodney, Chester and Chief was 50, 40, and 30%, respectively; the calculated DMD for aspen was 51.4, 46.8 and 30.5% for these animals, respectively. Since a complete chemical analysis of both the feed, aspen, and fecal material from this trial was not available for this report, we are not sure which trend is real and which is spurious.

Dry matter digestion of the mixed browse diet in Trial 4 using three moose had a mean digestibility of $39.7 \pm 4.5\%$. The dry matter ratio of birch:willow:aspen was 34.4:33.1:32.4 which was close to the percentage fed as wet weight. No energy determinations were available for this report.

Rumen Turnover

Rumen turnover time and rate of passage of food through the digestive tract was measured using radio-isotope tracers. Ruthenium 103 was used to label the solid portion and Chromium 51 the liquid portion of the digesta (see Schwartz and Franzmann 1981a,b for details of methods). The MRC Special had a rumen turnover time of 22.2 ± 3.8 hours for solids and 17.0 ± 3.3 hours for the liquid portion of the rumen contents. Turnover time for moose fed MRC Special plus clipped aspen (Trial #3) were similar with 20.4 ± 1.7 and 18.8 ± 1.4 hours for the solid and liquid materials of the rumen respectively (Table 7).

Energy Expenditure

The experimental procedure used to measure heat production in the metabolic chamber was modified three times during the first year as our knowledge and experience increased. Procedures have remained constant since March 1981 and no changes are anticipated. The only major change was in the length of each trial (individual measurement period). All trials during the first four series of experiments lasted for 2 hours (Table 8). Data collected during these trials were consistent and values of heat production within the expected range. However, the moose never laid down during any of the 32 trials, probably due to the narrow width of the chamber. It was important that moose lie down during some trials so we could measure the energy cost of standing versus lying. The chamber was enlarged in July 1980 to encourage the moose to lie down (see Appendix A).

Table 7. Rumen solid and liquid turnover rates of moose fed a pelleted ration and a mixture of pelleted ration and winter-clipped aspen in different digestion and balance trials in winter.

Animal	Ration	Body wt (kg)	Dry matter		DMD %	First appearance		Turnover time	
			intake (g/kg ^{0.75} / day)			(h)		(h)	
						Liquid	Solids	Liquid	Solids
Chief	MRC Special	351	--	--	--	--	14.2	19.7	
Chester	MRC Special	343	--	--	9	10	21.8	27.5	
Rodney	MRC Special	355	--	--	17	18	16.1	22.2	
Angel	MRC Special	363	--	--	14	16	16.0	19.3	
$\bar{x} \pm SD$		353 \pm 8.3	--	--	13.3 \pm 4.0	14.7 \pm 4.2	17.0 \pm 3.3	22.2 \pm 3.8	
Lucy	28:72 Aspen feed	363	54.3	61.7	10	17.2	10	18.5	
Chester	40:60 Aspen feed	334	69.6	59.5	10	19.4	10	20.8	
Rodney	50:50 Aspen feed	341	46.5	60.4	10	19.9	10	21.8	
$\bar{x} \pm SD$		346 \pm 15.1	56.8 \pm 11.8	60.5 \pm 1.1	10	18.8 \pm 1.4	10	20.3 \pm 1.7	

Table 8. Summary of heat production trials conducted at the MRC from December 1979 to May 1981.

No.	Date of trial	Length trial (h)	Number moose		Age of moose (mo)	Items* measured
			<u>measured</u>			
			ON feed	Fasted		
1	Dec. 1979	2	5	5	18	HP
2	March 1980	2	4	4	22	HP
3	May 1980	2	4	4	24	HP
4	June 1980	2	3	3	25	HP
5	Sept. 1980	5	3	6	28	HP, Position
6	Nov. 1980	24	1	-	29	HP, CH ₄ , Position
7	Dec. 1980	24	1	-	29	HP, CH ₄ , Position
8	Feb. 1981	24	2	2	32	HP, CH ₄ , Position
9	March 1981	12	3	3	33	HP, CH ₄ , Position
10	April 1981	12	4	4	34	HP, CH ₄ , Position
11	May 1981	12	3	3	35	HP, CH ₄ , Position

HP = heat production

Position = energy cost standing versus lying

CH₄ = methane production

Trials during the next three sets of experiments were 24 hours in length. Data collected included heat production, methane production, and cost of standing. Analysis of data from these 15 trials indicated that 12-hour trials provide information as accurate and precise as 24-hour trials. Since March 1981, all trials have been 12 hours in length (Table 8).

The normal sequence of events during an experiment is (1) measure food intake and digestibility for 7 days, (2) measure gas exchange for 12 hours with access to feed, (3) fast moose for 48 hours, (4) repeat gas measurements for 12 hours with moose in fasted condition. This procedure was altered during rut when males refused food and just prior to calving to avoid stressing the females.

2-Hour Trials

Variation in heat production during the 2-hour trials was due to differences in metabolic rates among moose, but mostly due to the amount of animal movement (standing quietly versus pawing floor, swinging head, etc.). Values in December were consistent because all moose displayed similar activity (Table 9). The March 1980 trials had large variations in heat production because some animals stood quietly while others were active. Activity was more consistent during the May and June trials. These data demonstrated the necessity of eliminating variation due to activity in order to compare heat production between seasons, age classes, and while consuming different types and amounts of forage. The only solution was to measure heat production while the moose were lying down because it is impossible to quantify activity. Also, fasting metabolic rate (FMR) values must be obtained when animals are lying down in order to make valid interspecies comparisons.

Our plan was to conduct energy trials for 24-hour periods, collecting expired gas in separate spirometers when moose were lying and standing. The cost of standing would be calculated for each moose and heat production values for the 2-hour trials could be corrected for standing. After rebuilding the chamber, 24-hour trials were conducted on four moose. The 24 hours were divided into two 12-hour periods due to limited capacity of spirometers. Cost of standing was calculated by

$$\frac{\text{HP standing} - \text{HP lying}}{\text{HP lying}} = \% \text{ increase due to standing.}$$

Values for cost of standing varied from 2.2 to 69.4%. The 2.2 is very likely a measurement error, but even omitting this value the cost of standing ranged from 18.2 to 69.4% (Table 10). The large difference was due to activity of the moose. The HP measured while standing included any movement by the moose. Calm moose with minimum movement had a cost of standing about 25% above HP when lying. However, cost of standing differed greatly between trials with the same moose and average values are not acceptable for correcting HP values. Heat production when lying down must be measured or calculated for each trial. Standard correction factors based upon an average cost of standing are not valid due to activity.

Table 9. Heat production (HP) and respiratory quotients (RQ) during 2-h energy trials in fed and fasted condition between December 1979 and June 1980.

Animal	Kcal/kg ^{.75} /day											
	December 1979				March 1980				May 1980			
	Fed	RQ	HP	Fasted	Fed	RQ	HP	Fasted	Fed	RQ	HP	Fasted
Rodney	256	1.06	196	.85	149	1.03	144	.71	195	1.05	160	.76
									212		1.76	182
												.71
Chester	256	.98	176	.87	233	.94	127	.74	166	.99	156	.80
									206		2.04	195
												.81
Chief	234	1.06	198	.82	229	.90	204	.72	218	1.01	179	.79
									232		1.87	242
												.78
Lucy	243	.98	183	.76	224	.94	208	.75	233*	1.02	191*	.77
\bar{x}	247	1.02	188	.82	209	.95	171	.73	203	1.02	172	.78
									217		1.9	206
												.77
$S\bar{x}$	10.8	.05	10.5	.05	40	.06	41.3	.02	29.2	.03	16.4	.02
									13.6		.14	31.6
												.05

* Moose in late stage of pregnancy.

Table 10. Heat production of moose during 24-hour trials at the MRC.

	HP (kcal/kg ^{.75} /day)					
	Chester	Rodney	Lucy	Lucy	Chief	Chief
	Nov 80	Dec 80	Feb 81	Feb 81	Feb 81	Feb 81
	Fed	Fed	Fed	Fasted	Fed	Fasted
1st 12-h period						
overall average	174	161	146	128	176	120
Standing only	193	174	162	131	194	140
Lying only	142	139	137	128	145	114
% time standing	68.7	49.6	40.5	36.3	63.2	25.9
Increased cost of						
standing, %	35.9	25.2	18.2	2.2	33.8	22.8
2nd 12-h period						
overall average	172	192	133	124	151	130
Standing only	195	205	151	156	181	143
Lying only	152	121	122	108	122	106
% time standing	53.7	59.6	37.5	33.3	49.9	62.2
Increased cost of						
standing, %	28.3	69.4	23.8	44.4	48.2	35.2

The procedure used at this time was to run a 12-hour trial. One spirometer was used to collect expired gases for the entire trial and another spirometer used to break the 12-hour trial into six 2-hour periods. The activity (standing or lying) was recorded throughout the trial. Often the moose would lie down during one or more complete 2-hour periods within a 12-hour trial. If not, regression analysis was used to calculate the HP while lying from HP during the 2-hour period and % time lying during each period. This method has worked well (Table 11); it provides a valid HP while lying down, the cost of standing, and the average HP for 12 hours is useful in examining seasonal cycles in HP.

Twenty-nine trials have been conducted in this manner. In most trials a value for heat production while lying can be predicted with a high degree of reliability (R^2 vary from .72 to .99, Table 11). The moose must be in a lying position for a significant portion of the trial in order to get reliable results. This method of calculating the resting metabolic rate removes the effects of varying activity levels between trials.

Seasonal Variation in Metabolic Rate

Data collected to date indicate that the metabolic rate of moose declines during winter and reaches a low point in early spring prior to initiation of plant growth (Fig. 3). The period of highest metabolic rate has not been pinpointed but it appears to occur in late fall, a period of rapid weight gain due to fat accumulation.

Heat Increment

Preliminary data analysis indicate that HI averages about 10% of the FMR. Seasonal trends and variation with diet have not been examined.

Methane Production

The pattern of methane production in relation to time of eating and body position is shown in Fig. 4. Peak production occurred about 20 minutes after eating. Production increased slightly when the moose laid down. This is contrary to the pattern shown by sheep and cattle where methane production increases with activity (Blaxter 1962). The general pattern of high production after a meal with a gradual decrease is similar to domestic ruminants.

Methane production has been measured in 16 trials of 12-hour duration. Three trials were conducted with a diet of browse (1/3 each of aspen, birch and willow CAG stems); the remaining trials were on the MRC Special diet. Energy lost as methane is usually expressed as the percent lost relative to gross energy intake. Ruminants usually produce more methane on a high energy, high digestibility diet and have a reduced loss when feeding on roughage. The moose lost about 6% of GE intake as methane when consuming the MRC Special (Table 12). Energy lost as methane when consuming browse was only 2%. This is a lower value than expected based on domestic livestock literature.

Table 11. Heat production values of moose during 12-hour trials with 2-hour periods and equation used to calculate HP while lying.

		Lucy		Lucy		Lucy		Lucy		Chief		Chief		Chief	
		Feb 81, fed		Feb 81, fed		Feb 81, fast		Feb 81, fast		Feb 81, fed		Feb 81, fed		Feb 81, fast	
Period	HP	up	HP	up	HP	up	HP	up	HP	up	HP	up	HP	up	HP
12-h \bar{x}	146	40	133	38	128	36.3	124	33.3	176	63.2	151	49.9	120	25.9	
1	193	100	100	0	159	46.7	102	12.5	254	100	105	0	130	59.2	
2	177	69	134	18	121	18.3	90	0	235	100	123	33.0	99	0	
3	128	0	170	92	153	69	90	0	208	87.5	201	100	146	57.5	
4	126	0	120	17	89	0	155	95.8	149	41.7	207	100	100	0	
5	182	79	109	4	147	47.5	159	58.3	125	26.7	135	11.7	111	39	
6	168	58	-	-	-	-	-	-	116	27.5	146	54.2	86	0	
Calculated \bar{x}															
equation															
		$y=1.46x-186.5$		$y=1.31x-140$		$y=.87x-79.9$		$y=1.13x-103$		$y=.595x-43.7$		$y=.985x-100$		$y=1.21x-109.9$	
R^2	.99	.92			.85		.87		.97		.92		.84		
Predicted															
lying															
value	127	106			91		91		73		102		90.5		

Table 11 - Continued.

Chief		Chief		Angel		Angel		Chester		Chester		Rodney	
Mar 81, fast		Mar 81, fast		Mar 81, fed		Mar 81, fast		Mar 81, fed		Mar 81, fast		Mar 81, fed	
% time		% time		% time		% time		% time		% time		% time	
Period	HP	up	HP	up	HP	up	HP	up	HP	up	HP	up	HP
12-h \bar{x}	109	40.7	94	33	134	35	109	28	142	74	126	87	126
1	148	100	88	0	156	67	103	17	175	100	115	100	158
2	136	66	82	0	112	6	115	33	151	42	116	100	110
3	117	44	86	55	134	32	83	0	145	84	92	100	129
4	111	26	80	0	102	0	114	25	130	100	94	100	113
5	89	0	102	41	146	54	89	8.3	144	100	134	100	124
6	98	8	119	100	159	50	168	88	120	17	107	21	110
Calculated \bar{x}									124	-	108		
equation													
$y=163x-148$		$y=3.33x-184$		$y=1.11x-115$		$y=1.02x-86$		$y=.89x-55$		$y=.17x-67$		$y=1.29x-117$	
R^2	.96	.74	.92	.98	.22	.016	.70						
Predicted													
lying													
value	90.5	79		104	84	62	-	90					

Table 11 - Continued.

		Rodney		Angel		Angel		Rodney		Rodney		Lucy		Lucy	
		Mar 81, fast		Apr 81, fed		Apr 81, fast		Apr 81, fed		Apr 81, fast		Apr 81, fed		Apr 81, fast	
		% time		% time		% time		% time		% time		% time		% time	
Period	HP	up	HP	up	HP	up	HP	up	HP	up	HP	up	HP	up	HP
12-h \bar{x}	109	78	176	60	171	54	134	67	144	100	178	71	166	83	
1	113	100	265	100	229	100	128	88	131	100	208	100	170	100	
2	114	62	145	0	179	50	126	54	132	100	211	100	179	100	
3	102	100	148	29	143	29	135	75	143	100	218	92	167	66	
4	105	100	145	17	199	42	129	75	147	100	168	42	156	50	
5	100	50	186	29	128	12	148	100	131	100	200	95	186	100	
6	114	56	145	25	189	70	137	46	173	100	130	0	-	-	

Calculated \bar{x}

equation

$$y = .44x - 126 \quad y = .67x - 83 \quad y = .76x - 84.7 \quad y = 1.06x - 69 \quad y = 1.197x - 155 \quad y = 1.76x - 220$$

 R^2

$$- \quad .89 \quad .82 \quad .18 \quad .96 \quad .74$$

Predicted

lying

value

$$58 \quad 122.7 \quad 111 \quad 65 \quad 129 \quad 124$$

Table 11 - Continued.

Period	Chester		Chester		Rodney		Rodney		Chester		Rodney		Rodney	
	Apr 81, fed	% time	Apr 81, fast	% time	May 81, fed	% time	May 81, fast	% time	May 81, fed	% time	Jul 81, fed	% time	Jul 81, fast	% time
HP	up		HP	up	HP	up	HP	up	HP	up	HP	up	HP	up
12-h \bar{x}	199	99	208	98	195	63	164	67	187	63	198	100	184.1	49.6
1	190	100	216	100	147	33	164	100	217	100	184	100	175.5	37.5
2	214	100	236	100	182	93	174	100	217	100	210	100	-	172
3	179	100	228	100	215	100	143	42	195	58	209	100	247.1	100
4	206	100	160	89	282	100	196	79	186	96	203	100	172.6	10
5	198	92	159	100	170	12.5	139	8	193	78	192	100	207.4	72
6					180	39	147	71	144	0	-	178	77	-
Calculated \bar{x}														
equation	-		-		$y = .59x - 52$		$y = 1.09x - 109$		$y = 1.3x - 177$		$y = 1.03x - 150.3$		$y = 1.04x - 123$	
R^2					.508		.45		.80		.88		.867	
Predicted														
lying														
value					89		99		136		145		134	

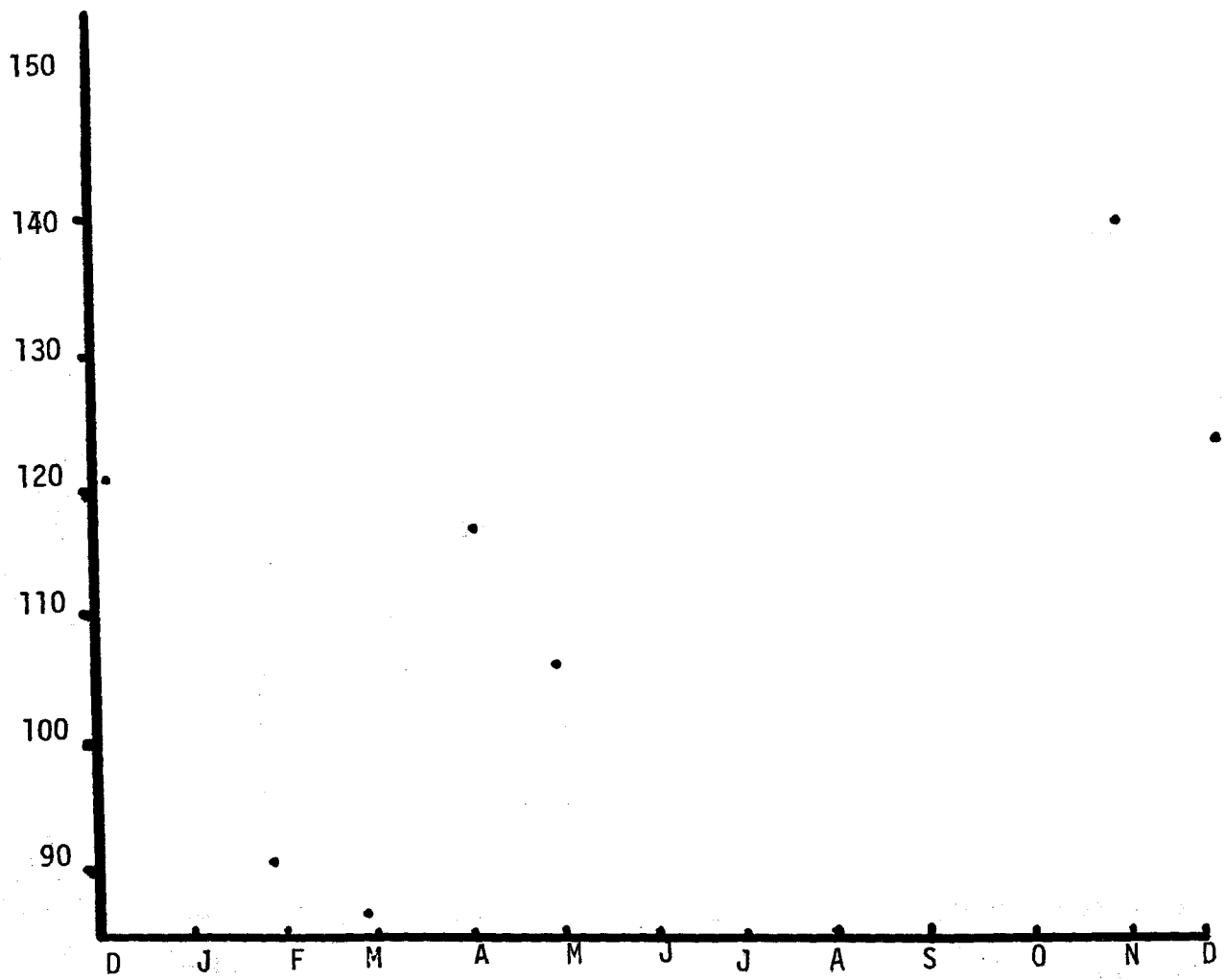


Fig. 3. Seasonal metabolic rate of moose while fasted and lying.

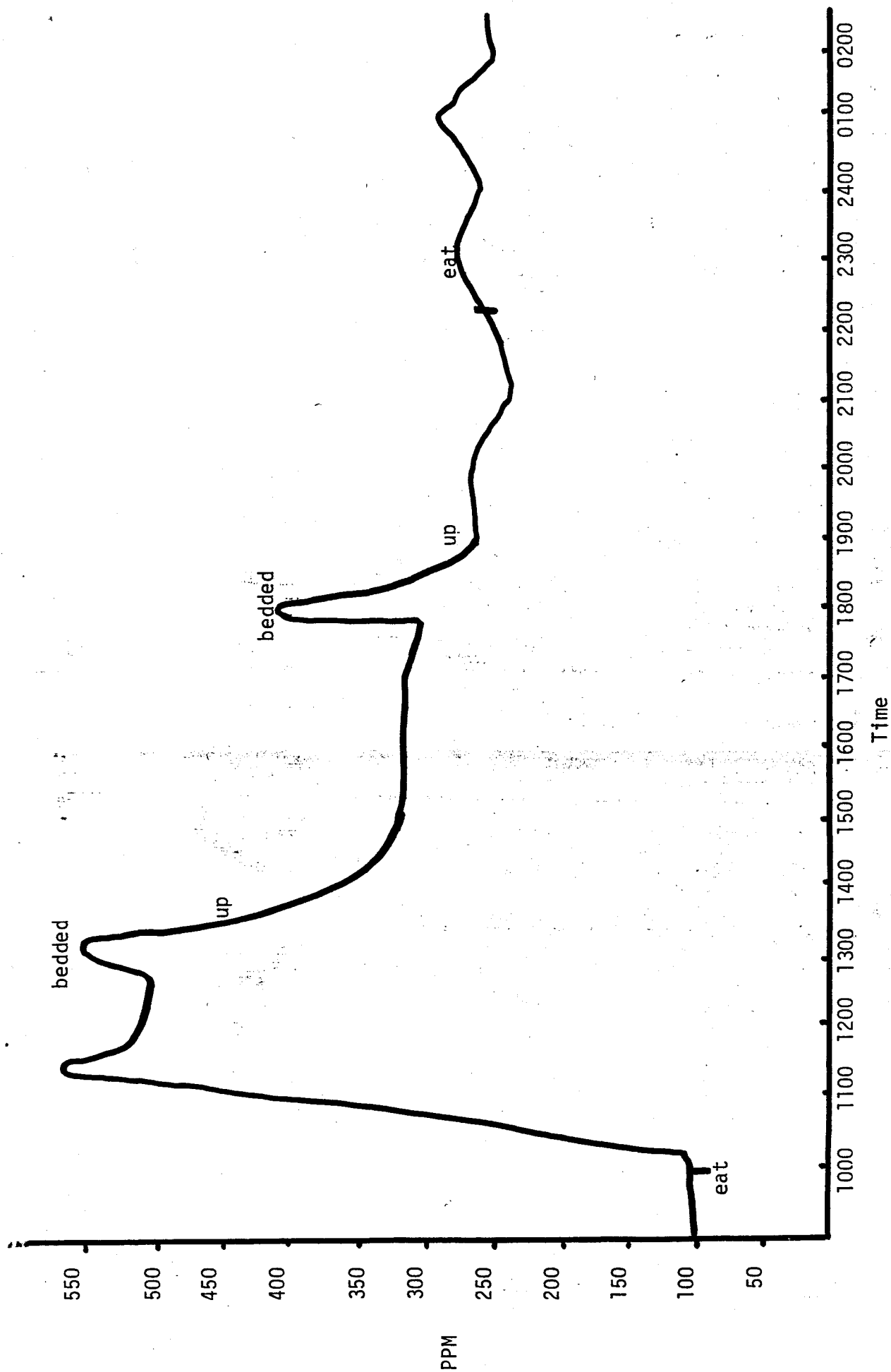


Fig. 4. Pattern of methane production over an 18 hour period by a moose fed a pelleted ration. Moose was a 2.5 year old male, fasted 8 hours prior to start of the trial.

Table 12. Food intake and methane production of moose on a 24-hour basis.

Date	Moose	Diet	Intake DM g	kcal/ g	GE intake	CH ₄	kcal CH ₄	% GE lost
Nov 80	Chester	MRC	4037	4.35	17561	117.8	1119.1	6.37
Dec 80	Rodney	MRC	4478	4.35	19478	105.4	1001.3	5.14
Mar 81	Rodney	Browse	4798	5.10	24497	42.5	403.8	1.65
Mar 81	Chester	Browse	4226	5.10	21573	37.9	360.0	1.67
Mar 81	Angel	Browse	2276	5.10	11618	34.9	331.6	2.85
Apr 81	Angel	MRC	5171	4.17	21584	108.2	1027.9	4.76
April	Chester	MRC	5467	4.17	22820	140.8	1337.6	5.86
April	Lucy	MRC	3752	4.17	15662	98.0	931	5.94
April	Rodney	MRC	3476	4.17	14510	88.6	841.7	5.80
May	Rodney	MRC	5563	4.17	23222	146.6	1392.7	5.99
May	Chester	MRC	3934	4.17	16421	129.9	1234.0	7.51
May	Chief	MRC	4303	4.17	17962	134.2	1274.9	7.10

Energy Partitioning

The flow of food energy through the moose can be quantified by combining data from the digestion trials and heat production trials. The gross energy (GE) in forage can be partitioned into several basic components:

Digestible energy (DE) = GE - energy in feces

Metabolizable energy (ME) = DE - energy in urine and energy lost as methane

Net energy (NE) = ME - heat increment.

The energy partitioning of three moose fed a mixture of current annual growth twigs of aspen, willow, and birch is shown in Tables 13 and 14. These trials were conducted in mid-March. They show the moose were in negative energy balance. The deficit of energy was not severe for any of the moose. Energy balance can be achieved by increasing forage intake by 1.06 to 2.01 kg of dry weight per day. However, the rate of passage of food through the digestive tract and rumen volume influence forage intake. The moose may not be capable of processing more food of such low quality (34.5% DM digestibility). These factors will be examined in later stages of this study.

Carrying Capacity Model

Results for the baseline run with adult female moose (Table 15) indicated a 21.6% loss of total body weight, an 85.9% loss in total fat reserves, and less than 1% loss of lean body tissue. Total body weight loss was similar to losses for mule deer (Odocoileus hemionus) (19%) and elk (Cervus elaphus) (17%) for similar simulation runs (Swift et al. 1979) and was slightly higher than weight loss for adult female moose (17%) examined by Franzmann et al. 1978 at the Moose Research Center.

Percentage of fat lost was slightly lower for moose than that for deer and elk (91.2% for both) reported by Swift et al. (1979). We were unable to find any information on body composition of moose and therefore our estimate of 24.5% total body fat (Table 1) may have been an overestimate. Reduction of total body fat to 14.3% in the simulation run (Table 15), however, resulted in a 100% loss of total body fat over the winter.

The less than 1% decrease in lean body mass for moose was much lower than that for deer (-6.1%) and elk (-3.6%) (Swift et al. 1979). By reducing total body fat to 14.3% the loss of lean body tissue increased to 17.6% for moose also indicating that initial fat reserve estimates of 24.5% were probably too high. These simulations indicated that we need to measure the total body fat for moose to improve our estimates in the simulation model.

Increasing total fat reserved to 33.3% of total body weight (Table 15) resulted in similar change in total weight loss through the winter (-23.8%) when compared to baseline data (-21.6%). Total fat reserves declined

Table 13. Gross energy (GE) partition in three adult moose fed browse in March at the Moose Research center, Alaska.

	Rodney		Chester		Angel	
	kcal	% GE	kcal	% GE	kcal	% GE
GE intake/day,	17649	100	20468	100	15347	100
Fecal energy/day	9968	56.5	13350	65.2	10009	65.2
Urine energy/day	1033	5.85	1328	6.48	910	5.93
Methane energy/day	291	1.65	342	1.67	437	2.85
Heat increment	1518	8.60	1401	6.85	1832	11.94
Digestible energy	-	43.5	-	34.8	-	34.8
Metabolizable energy	-	36.0	-	26.6	-	26.0
Net energy	-	27.4	-	19.8	-	14.1
Net energy/DM (kcal/g)	-	1.40	-	1.01	-	0.72

Table 14. Daily intake of energy by three adult moose fed browse in March at the MRC, Alaska.

	Rodney	Chester	Angel*
Gross energy (GE) (kcal)	17649	20468	15347
Gross energy/kg $W^{.75}$	197.5	233.67	167.54
DE/kg $W^{.75}$	85.9	81.3	58.3
ME/kg $W^{.75}$	71.1	62.2	43.5
Net energy/kg $W^{.75}$	54.1	46.2	23.6
Fasting heat production in chamber	93	93	84
Energy deficiency kcal/kg $W^{.75}$	21.9	30.8	40.5
Energy deficiency (kcal)	1957	2698	3710
Additional food to eliminate deficit (kg)	1.06	1.46	2.01

*Pregnant animal, produced one calf May 27, 1981.

Table 15. Results of simulation experiments with adult female moose in winter.

	Change in wt (%)	Change in lean (%)	Change in fat (%)
Baseline run	-21.6	-0.16	-85.9
Activity costs increased (20%) to 1.6 BMR	-24.5	-0.18	-97.8
Activity costs decreased (20%) to 1.4 BMR	-18.3	-0.17	-72.9
Initial fat weight decreased (50%) to 51 kg (14.3% total body wt)	-29.4	-17.6	-100
Initial fat weight increased (50%) to 153.2 kg (33.3% total body wt)	-23.8	-0.20	-71.0
Dietary nitrogen increased by 10%	-21.9	-0.14	-87.2
Dietary nitrogen decreased by 10%	-21.3	-0.19	-85.6
Diet digestibility increased by 10%	-16.3	-0.17	-64.8
Diet digestibility decreased by 10%	-31.3	-8.4	-100
Metabolic fecal nitrogen 7.6 g/kg (Robins et al. 1974)	-28.5	-7.3	-92.0

71.0% for the "fat" moose vs the baseline moose (-85.9%). Loss of lean body tissue was similar for both runs. These changes reflect similar energy demands through the winter, resulting in near identical losses in the percentage of total weight. As discussed by Swift et al. (1979), experimental runs in which initial fat reserves were increased and decreased by 50% yielded the expected result that condition at the start of winter is an important determinant of over-wintering success. Good estimates of winter range capacity cannot be made without taking into consideration the ability of summer and transitional ranges to provide adequate nutrition.

Changing activity costs by +20% had a marked effect on moose condition change over the winter. Baseline activity costs in the baseline run were estimated as being 50% of basal metabolic costs. The 20% changes therefore resulted in activity costs of 40% and 60% of basal metabolic costs. It is unlikely that activity costs for wild ruminants can be estimated more precisely than this at present (Swift et al. 1979). Changing activity costs had little effect on lean body mass, but caused large changes in body fat and total body weight (Table 15).

Changing the dietary nitrogen content by +10% had almost no response in tissue weights when compared to the baseline run. These results indicate that the dietary nitrogen concentration was probably above the minimum daily requirements. The animal was thus in positive nitrogen balance.

Very large responses were observed to changes in the digestibility of the diets. An increase by 10% of the baseline values had the largest positive impact on fat reserves of any experimental run. Reducing digestibility by 10% caused a total depletion of fat reserves, and 8.4% loss of lean body tissue, and a 31.3% loss of total body weight. The changes imposed on digestion of dry matter (+10%) were not large and well within the range expected to occur due to annual variation in forage quality, quantity, and availability.

Changing the amount of nitrogen lost in the feces from 5 g/kg food intake to 7.5 g/kg intake as reported for deer by Robins et al. (1974) had a marked effect on the loss of lean body tissue. There were also increased losses of fat and total body weight (Table 15).

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APPENDIX A

RESPIRATION CHAMBER FOR STUDY OF ENERGY EXPENDITURE OF MOOSE

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Abstract: The respiration chamber and associated equipment used at the Kenai Moose Research Center to measure energy expenditure of moose is described. Methods used to construct the chamber and to measure respired gas volume and composition are discussed.

Partitioning the flow of energy through a ruminant animal requires a measurement of energy lost in feces, urine, respiratory gases and as heat increment (HI). Fecal and urinary energy loss can be sampled and measured with standard digestion cages and routine laboratory analysis. Determination of energy lost as methane and HI requires a means of measuring the exchange of respiratory gases or production of heat. Direct measurement of heat flux is difficult and requires close confinement of the animal. Indirect calorimetry is the method used most often with large bodied animals. This technique estimates metabolic heat production from the amount of oxygen consumed and carbon dioxide

produced (Kleiber 1961, Blaxter 1967).

A respiration chamber or face mask can be used to collect respired gases. Systems involving a chamber can be closed-circuit, in which air is recirculated through the system, or open-circuit in which fresh air is continuously circulated through the system. The open-circuit indirect calorimetry method has great versatility. Animals can be confined in the chamber for long periods, allowing a wide variety of experimental procedures. We describe the open-circuit respiration chamber and gas analysis equipment used at the Kenai Moose Research Center in Alaska. Our system is similar to that used at the Ritzman Laboratory, University of New Hampshire (Haven Hayes, pers. comm.). Several alterations have been made to adapt it to moose and low temperatures in Alaska.

THE CHAMBER

The respiration chamber measures 2.4 X 2.3 X 2.2 m in size with a 0.9 X 0.9 X 2.2 m addition in one corner to accommodate a refrigeration unit and feed bunk (Fig. 1). The chamber was constructed of 5 X 20 cm floor joists and 5 X 10 cm wall and ceiling joists covered with high quality 1.9 cm plywood fastened with screws. A subfloor of plywood slopes to the center and one end to aid urine flow out of the chamber. The moose stand or lie on a floor of expanded sheet metal suspended 5 cm above the sloping subfloor. The expanded metal has holes of sufficient size to allow feces and urine to pass through thus maintaining a clean, dry floor. Seven plexiglass windows (30 X 76 cm) were placed in the chamber walls. The entry door is 1 X 2.1 m; it fits tightly against rubber material to prevent air leaks. All joints and screw holes were sealed with silicone sealer and all interior walls were painted with

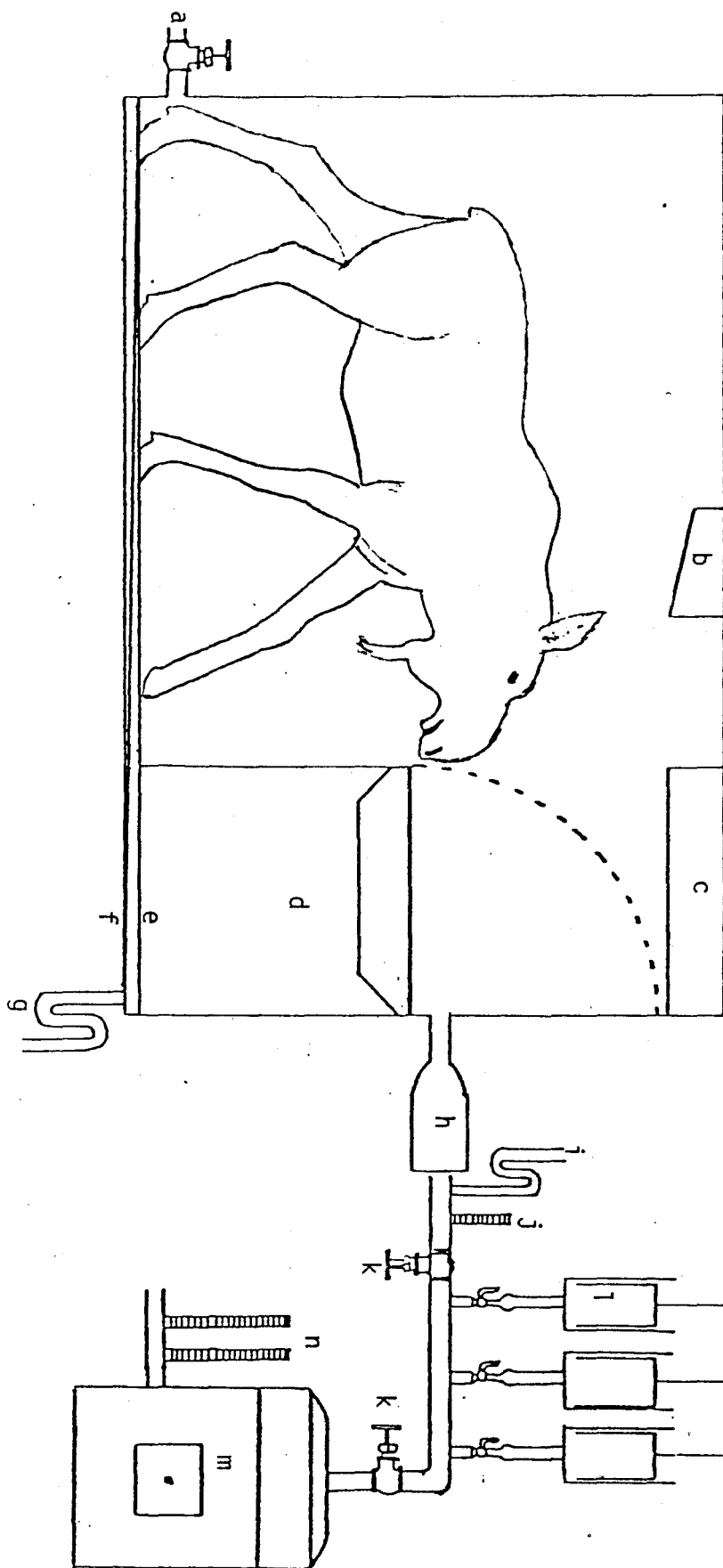


Fig. 2. Schematic drawing of the respiration chamber and gas handling system at the Kenai Moose Research Center. Alaska. a, air inlet valve; b, heater; c, refrigeration unit; d, feed bunk; e, expanded metal floor; f, sloping subfloor; g, urine drain; h, vacuum cleaner; i, manometer; j, line thermometer; k, pressure valve; l, spirometers; m, gas meter; n, wet and dry thermometers.

several coats of epoxy paint to prevent air leakage.

Humidity in the chamber is controlled by a refrigeration unit¹ suspended from the ceiling (Fig. 2c). This unit maintains relative humidity at about 30% and temperature between 2 and 4 C. It has a fan that continuously mixes the chamber air. Air is moved at less than 1 m/sec. This velocity does not increase heat loss (Moen 1973). Water vapor removed by the refrigeration unit is drained outside the chamber. A thermostatically-controlled electric heater² (Fig. 2b) warms the air during winter so the refrigeration unit will function. Walls, floor and ceiling are insulated with fiberglass. A feeding stall with a remote control access door (Fig. 2d) is located below the refrigeration unit. Food can be added or removed without entering the chamber.

Air volume of the chamber is 13,200 liters. Volume can be reduced to accommodate smaller animals by displacing air with large air mattresses. Chamber volume should be as small as possible without distressing the experimental animal. This allows CO₂ level in the chamber to increase to about 1% rapidly and provides a faster response to changes in respiratory gases due to animal activity.

Outside air enters the chamber through a 4.5 cm valve (Fig. 2a). The entry valve is partially closed to keep the chamber at a slight negative pressure. This insures that any air leaks will be into the chamber and that no gas expired by the moose can escape.

¹Model M100, Nor-Lake Inc., Hudson W.I. 54016

²Glassheat, K&L Contruction, Soldotna, AK

GAS MEASUREMENT

Gas is pumped out of the chamber at a constant rate by a reversed vacuum cleaner motor³. The flow rate is regulated by a rheostatic control of the vacuum cleaner motor. Flow rate for an adult moose is 280 l/min. This rate maintains the CO₂ level inside the chamber between 0.5 and 1.0%. Values within this range can be measured accurately; animals can tolerate a CO₂ level as high as 2.0% without any respiratory stress. The gas is pumped into a 5.1 cm plastic line and through a gas meter⁴ that measures total volume to the nearest liter (Fig. 2m). Pressure in the gas line is kept slightly positive by a valve placed in front of the gas meter. The positive pressure permits aliquot subsamples to be collected continuously in three 9 liter spirometers⁵ (Fig 2). Needle valves in the flow line to each spirometer enable the collection of the aliquot samples over 2- to 24-hour periods. Gas is dried by passing it through CaCl₂ and filtered through glass filter paper prior to entering the spirometers. A stopcock valve in the main flow line (Fig. 2k) permits continuous analysis of the gas throughout the trial. This line bypasses the spirometers and flows directly to the gas analysis equipment after the gas has been dried and filtered.

Temperature and moisture content of the gas is monitored by wet and dry bulb thermometers. Barometric pressure is measured with a standard

³ Model L, Electrolux Co., Stanford, CT

⁴ Model AL1400, American Meter Co., Philadelphia, PA

⁵ Warren E. Collins, CO., Braintree, MA

mercury barometer. All gas volume measurements are converted to standard temperature and pressure before any calculations are made. Air pressures inside the chamber (negative) and in the main flow line (positive) are monitored by simple home-made manometers.

Composition of the gas is determined by passing it through three instruments that measure the content of oxygen, carbon dioxide and methane (CH_4). Oxygen is measured by a paramagnetic analyzer⁶ to the nearest 0.01%. CO_2 ⁷ and CH_4 ⁸ by non-dispersive infrared analyzers-- CO_2 to the nearest 0.01% and CH_4 to the nearest 0.0001%. The instruments are connected so that the same gas sample flows through each one. Gas from the spirometers or directly from the main flow line passes through each machine at a constant rate of 500 ml/min.

The instruments are calibrated every hour during a trial using gases of known composition. Three gas mixtures are used for calibration, one being outside air and the other two provided by a chemical supply company⁹ in compressed gas cylinders. The calibration gasses are pumped out of the spirometers at the same rate of flow as the respiratory gas.

All instrument readings are made manually. Automatic recording devices are available for all instruments, but they are expensive.

⁶ Model OM14, Beckman Instruments, Inc., Schiller Park, IL

⁷ Model LB2, Beckman Instruments, Inc., Schiller Park, IL

⁸ Model 865, Beckman Instruments, Inc, Schiller Park, IL

⁹ Scientific Gas Co., Denver, CO

Heat production is calculated by multiplying the volume of O_2 consumed during the trial by the thermal equivalent (caloric value) of the O_2 at the extant respiratory quotient (Brody, 1968). Energy expenditure is expressed in terms of heat production. Standard units of measure are either Kcal/24 hr or Kcal/Kg BW.⁷⁵ (Kg BW.⁷⁵ = Body weight of animal in Kg raised to the .75 power). The recent trend in Europe has been to express energy expenditure as kilo joules/24 hr. (1 kJ 0.239 Kcal).

DISCUSSION

The first chamber we built was 2.4 X 1.2 X 2.4 m and had only one small window, at one end. Adult moose had great difficulty in turning around and refused to lie down. They became agitated after a few hours of confinement. It was important that the moose remain calm in a recumbent position to enable accurate measurement of resting metabolic rates. We enlarged this chamber to its present size and added 5 more windows. The new dimensions provided adequate space for the moose to lie down and turn around but minimized movement. The windows helped keep the moose calm, especially if they could see other moose outside the chamber. The windows also allowed us to observe the moose and record their activity.

Because the expanded metal floor had a rough surface which we felt might injure the feet of the moose, we placed a 1.3 m² plywood board in the center of the chamber floor. The moose stand and lie on this board nearly all the time they are in the chamber.

We have conducted 48 energy expenditure trials in this chamber using six moose during the past 18 months. The age of the moose varied from 6 to 30 months. They were either in a fasted condition (no food for

48 hours) or on ad libitum food intake. Length of trials varied from 2 to 24 hours. The trials have been used to measure CH_4 production in relation to food intake, energy costs of standing and diurnal variation in energy expenditure. Seasonal changes in energy requirements have been examined. The measurements have a high degree to repeatability indicating the system is capable of producing precise results.

The respiration chamber has been operated at outside temperatures ranging from 35 to 20 C without problems. The electric heater warms the air sufficiently, even at extremely low temperatures, to make the refrigeration (dehumidifying) system operate. The cooling system easily lowers high air temperatures. The system does not have the capability to reduce chamber temperature or increase wind velocity to critical levels for moose.

The entire system cost \$17,000 excluding labor at 1979 prices. Of this total, the gas handling and gas analysis equipment cost \$14,000. The chamber with attachments cost \$3,000; about half of which was accounted for by the refrigeration system.

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